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Two new endemic species of *Chrysopodes* (*Neosuarius*) (Neuroptera, Chrysopidae) from the Galápagos Islands

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Abstract

Two new species that were previously undistinguished from the Galápagos endemic *Chrysopodes* (*Neosuarius*) *nigripilosus* (Banks), are described. These descriptions double, from two to four, the number of endemic green lacewing species known from the archipelago. The four species include: *Chrysoperla galapagoensis* (Banks), *Chrysopodes* (*N.*) *nigricubitus* **sp. n.**; *C.* (*N.*) *nigripilosus*; and *C.* (*N.*) *pecki* **sp. n.** Three of these species – *C.* (*N.*) *nigripilosus*, *C.* (*N.*) *nigricubitus* and *Chrysoperla galapagoensis* – each occur on more than one island, whereas *C.* (*N.*) *pecki* is known only from the summits of two craters on Isabela Island. A suite of very distinctive features differentiates the three Galápagos *Chrysopodes* (*N.*) species from their congeners on mainland South America. Subtle, but consistent characteristics separate the three Galápagos species from each other. The small degree of morphological divergence among the Galápagos lacewings is in marked contrast to the spectacular radiation of Hawaiian lacewings; the processes of diversification and speciation may differ significantly between the two island archipelagos.

Keywords

Galápagos Islands, endemic lacewings, geographic variation, new species

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Introduction

The diversity of insect species reported from the Galápagos Islands is relatively low (e.g., Linsley and Usinger 1966; Parkin et al. 1972; Peck 2001); this generalization appears true for the green lacewings (Chrysopidae). In the most recent synopsis of the Galápagos fauna, Peck (2001) listed only four species: (a) two endemics [*Chrysoperla galapagoensis* (Banks, 1924) and *Chrysopodes* (*Neosuarius*) *nigripilosus* (Banks, 1924)] and (b) two others with broad distributions in Central and South America [*Chrysoperla externa* (Hagen, 1861) and *Ceraeochrysa cincta* (Schneider, 1851)]. Both endemic species are known from several islands in the archipelago, and despite numerous scientific expeditions, no new endemic chrysopid species have been described since Neuroptera were first recorded from the Galápagos (Banks 1924).

For several reasons, we considered the possibility that additional species of chrysopids might occur on the islands. First, Banks' (1924) relatively brief description of *C.* (*N.*) *nigripilosus* was based on a small series of specimens from one island, and it was written before the systematic value of male or female genitalia were generally appreciated. Second, since Banks' original treatment of the Galápagos lacewings in 1924, a small but substantial number of specimens has accumulated in museums, but no further systematics work has ensued. Third, one of the endemic species [*C.* (*N.*) *nigripilosus*] is well differentiated from its closest relatives on the western South American mainland (Tauber, in press). This species' high level of differentiation and its broad inter-island distribution would be consistent with a relatively long evolutionary history on the islands. Given the relatively rapid rates of speciation among Hawaiian lacewings (Zimmerman 1957, Tauber et al. 2007), we hypothesized that cryptic species may be sequestered within the single recognized Galápagos *Chrysopodes* species. And, we thought it especially timely to examine this hypothesis during the celebration of Darwin's bicentennial.

To begin our study, we examined all of the *Chrysopodes* specimens originating from the Galápagos archipelago that we could obtain from museums and compared them with the types of *C.* (*N.*) *nigripilosus.* We found that these specimens share many external traits (general body color, size, head and wing features) and that they also have a common suite of genital characters that distinguish them from the other (mainland) species of *Chrysopodes* (*Neosuarius*) (Tauber, in press). Furthermore, our study revealed that the specimens express subtle variation that, for the most part, appears consistent with intraspecific (geographic) variation in *C.* (*N.*) *nigripilosus;* however, in two cases, the variation is strongly indicative of new species.

Here, we (1) re-describe *C.* (*N.*) *nigripilosus* from the type locality (Baltra) and (2) characterize the variation in the available specimens of this species from four other islands (Santa Cruz, Isabela, Fernandia, Santa Fe). Finally, (3) we describe two new *Chrysopodes* (*Neosuarius*) species that our study differentiated from *C.* (*N.*) *nigripilosus* – one from Santa Cruz and Pinta Islands, and another from two Volcánoes on Isabela Island.

Materials and methods

The *Chrysopodes* specimens from the Galápagos Islands that we studied came from the following collections: American Museum of Natural History, New York (AMNH), Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ), Bernice P. Bishop Museum, Honolulu (BPBM), California Academy of Sciences, San Francisco (CAS), National Museum of Natural History, Smithsonian Institution, Washington, D.C., formerly United States National Museum (USNM), the Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium (IRSNB) and the National Museum of Scotland, Edinburgh (NMS).

It is noteworthy that most of the pinned specimens that were available are relatively discolored. The discoloration is accentuated because the integument of *Chrysopodes* (*Neosuarius*) species tends to have a heavy coating of waxy material (probably an adaptation to arid conditions); often the coating becomes brownish over time. In contrast, the markings on the specimens that were stored in alcohol (those from the IRSNB) are well preserved and readily visible, in part because the waxy material was dissolved. Thus, our reports of head and body color relied heavily on the specimens preserved in alcohol; our observations from pinned specimens should be considered as estimates.

The procedures in this study followed those used previously (Tauber 2003, 2007; Tauber et al. 2008). In addition to the drawings and images published herein, others are available on the Morphobank website: http://morphobank.geongrid.org/permalink/?P344.

Chrysopodes (Neosuarius) of the Galápagos Islands

The Galápagos *Chrysopodes* (*Neosuarius*) are generally of a similar, relatively medium size; wing length ranges from ~10.2–13.7mm. They are also alike in coloration, i.e. tan to light brown bodies with darker brown mottled markings, cream-colored to light brownish heads with dark brown facial markings, hyaline wings with a relatively narrow costal area and white and dark brown venation in a typical *C.* (*Neosuarius*) pattern (Tauber, in press).

In the above, and several other internal and external traits, the Galápagos *Chrysopodes* (*Neosuarius*) are most similar to the *flavescens* group of *C.* (*Neosuarius*) species on the mainland (Tauber, in press). However, our study here shows that the Galápagos specimens share a suite of unique genital characters that distinguish them from the mainland species. For example, they are the only *C.* (*Neosuarius*) in which the males have a pair of large, eversible pouches (probably pheromonal) that extend posterolaterally from the membrane at the tip of the terminal abdominal sternite, and a pair of elongate, setose, ducts that originate within the gonosaccus (immediately below the mediuncus) (Figs 9c, 10c, 11c). The interior of the ducts appears grainy; the ducts may be glandular.

Like other species in the *flavescens* group, the Galápagos females have a distinctive, tubular spermatheca; the spermathecal duct is short and lightly sclerotized (Fig. 13). The bursa is leathery and moderately large (it covers the spermatheca), and the bursal glands are bulbous and bear elongate accessory ducts (Fig. 13). The spermathecae of the three endemic *Chrysopodes* (*N.*) species are unique in that they have a very small mesal swelling and are only slightly bent; they lack the bean-shaped enlargements, coils and sharp bends that characterize the spermathecae of the mainland species.

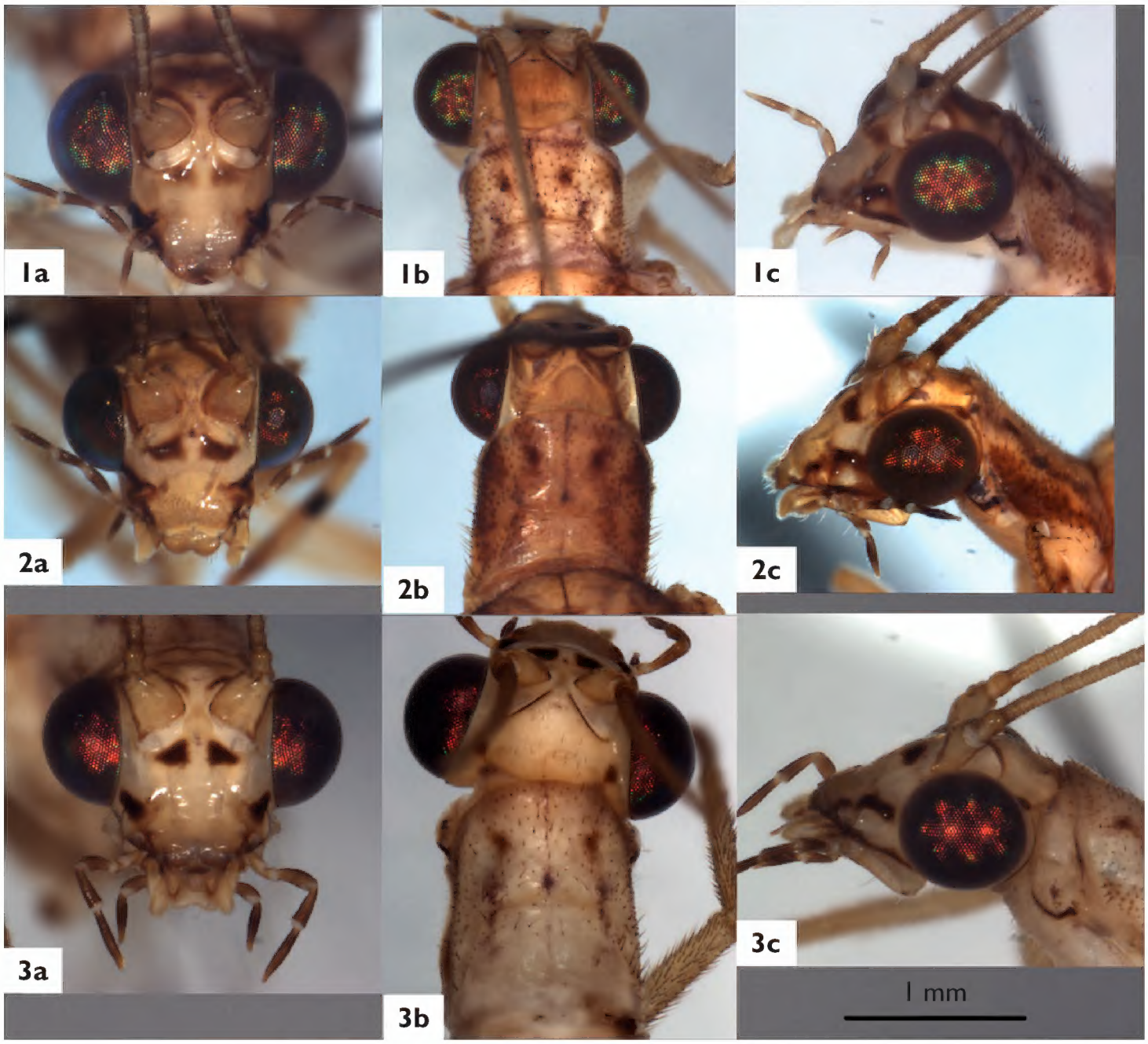
These numerous synapomorphies provide strong evidence that the extant *Chrysopodes* (*Neosuarius*) on the various Galápagos islands have a common evolutionary history of differentiation from an ancestral species that immigrated to the Galápagos from the South American mainland.

Chrysopodes (Neosuarius) nigripilosus (Banks, 1924)

Diagnosis. *Chrysopodes* (*Neosuarius*) *nigripilosus* specimens from the type locality (Baltra, = South Seymour; all pinned) are distinguished by their overall tan to light tan body color; the pleuron, venter and legs are largely light tan to cream-colored. The vertex is light brown and the facial markings range from light to dark brown (Fig. 1). The forewing membrane is without markings or suffusion; below the stigma there usually are three to four (occasionally two) crossveins between the Subcosta and Radius, (scx); and the second cubital crossvein (cux2) is not bent or crassate, nor does it have an enlarged swelling (Fig. 4a). The venter of the male abdomen is largely cream-colored to light tan throughout; in contrast, the female S5 and S6 are entirely brown, S7 is either brown entirely or basally, and the terminus is light to dark brown (Fig. 6a, b).

In the males: (a) the horizonal apodeme along the ventral margin of T9+ectoproct is arched and its posterior tip is bifurcated (see Note in brackets below); (b) the gonarcus is arcuate, with the gonarcal arms extending downward, not outward (Fig. 9b, c); (c) the eversible pouches at the tip of S8+9 are large and well separated mesally by a distinctly flat membrane (Fig. 8). In the female, the spermathecal duct is short and it lacks tight coils; the bursal glands are large and globose and their accessory ducts may be branched (Figs 13, 14). The subgenitale bears a pair of invaginated pouches that are near the base of the bursal glands; in *C.* (*N.*) *nigripilosus*, these pouches typically are flat and folded (Fig. 15a).

[Note: In Chrysopidae the apex of the abdomen is opened by two major apodemes articulating with each other at their bases. One apodeme runs along the ventral portion of tergite 9+ecoproct; it is termed the dorsal apodeme (d.a.). The other apodeme runs along the dorsum of sternite 8+9 and is termed the ventral apodeme (v.a.). The dorsal apodeme can be complex, with a dorsal branch (d.b.) along or below the anterior side of the callus cerci, a ventral branch (v.b.) that projects ventrally towards the gonarcus, and a caudal branch (c.b.) that extends distally below the callus cerci and can project beyond the ectoproct.]



Figures 1–3. Head and prothorax. **1** *Chrysopodes* (*Neosuarius*) *nigripilosus* **2** *C.* (*N.*) *nigricubitus* **3** *C.* (*N.*) *pecki*. (**a**) frontal view (**b**) dorsal view (**c**) lateral view. The scale applies to all images.

Description of specimens from type locality. *Head.* (Table 1, Fig. 1a, b, c): Vertex raised, flat, pentagonal shape, with small, upward fold posteriorly; surface of vertex with small, brown setae. Frons smooth, shiny throughout. Clypeus convex basally; surface smooth, mostly flat, very slightly raised in middle. Labrum flat, surface smooth; distal margin straight. Gena smooth, rounded. *Coloration:* Frons light tan to light brown with pair of brown, subtriangular to roundish marks below toruli; clypeus with lateral margins dark brown. Vertex brown. Toruli light brown, with surrounding sclerotized areas brown to dark brown; dorsal torulus with two dark brown, vertical streaks, larger one extending from below center of scape, smaller one extending from below mesal margin of scape. Genae dark brown, central area with large to small, longitudinal, pale stripe. Scapes light brown to tan, unmarked; pedicel brown basally, lighter distally; flagellum light brown. Maxillary palp: segments 3–5 brown; basal two segments tan. Labial palp with terminal segment brown, basal segments tan. Venter tan to cream-colored; lateral margins of submentum dark brown.

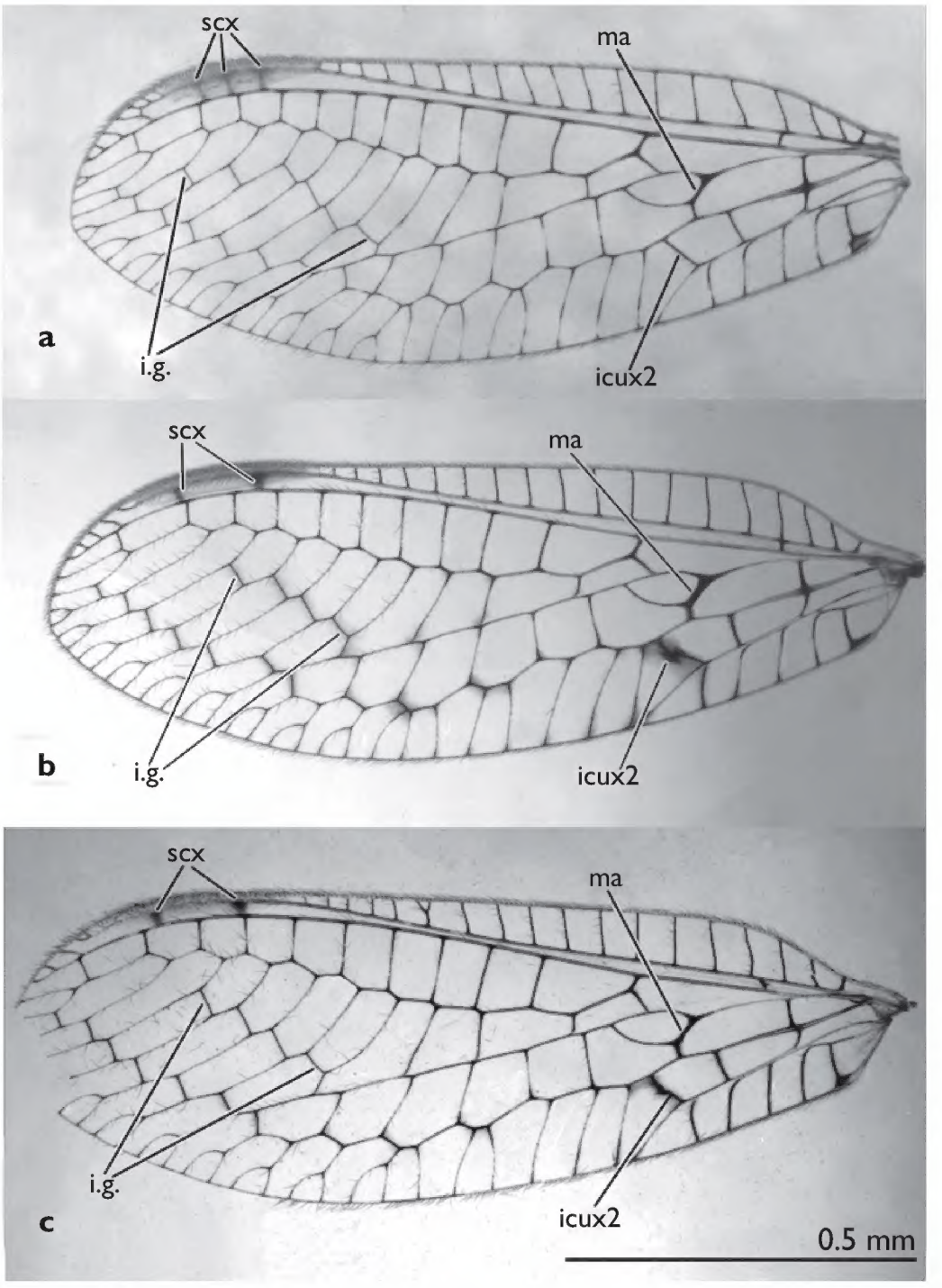


Figure 4. Forewing. **1** *Chrysopodes* (*Neosuarius*) *nigripilosus* **2** *C.* (*N.*) *nigricubitus* **3** *C.* (*N.*) *pecki*. **icux2**, second intracubital crossvein; **i.g.**, inner gradate veins; **ma**, median arculus; **scx**, subcostal crossveins (between subcosta and radius). The scale applies to all images.

Thorax. (Table 1, Fig. 1b). Pronotum tan to light brown, with scattered, brown, mottled markings sublaterally; several long, thin, pale setae laterally, short, robust, dark brown to black setae dorsally. Mesonotum, metanotum light brown mesally, brown laterally; setae on mesonotum short, robust, dark brown; setae on metanotum sparse, thin, pale. Pleural areas tan to cream-colored, sometimes with brown markings. Legs cream-colored without markings, setae light brown. Tarsal claws amber, long, narrow, with broad cleft, small base; area between claws black.

Wings. (Table 3, Figs 4a, 5a). Forewing about three times longer than tall, with apex broad, rounded; anterior margin relatively straight; posterior margin curved. Costal area narrow, greatest height ~0.17–0.18 times height of wing, tallest at costal cell (#5–6). Subcosta, radius (R) slightly sinuate; most costal veinlets, radial crossveins straight; one subcostal crossvein basally, three to four below stigma. Ten to twelve radial crossveins

Table 1. Range of variation in head and thoracic features among geographic populations of two *Chrysopodes* (*Neosuarius*) species from the Galápagos Islands.

	Chrysopodes (*N.*) *nigripilosus* (Banks)							
	Baltra	Santa Cruz	Isabela	Isabel	Isabel	Isabel	Santa Fe	Fernandina
	Type locality	Academy Bay	Puerto Villamil	Punta Tortuga	Volcán Wolf	Volcán Alcedo	5 m, Lagoon	Cabo Hammond
	(N=5)	(N=4)	(N=2)	(N=1)	(N=3, 2 alcohol)	(N=1)	(N=1, alcohol)	(N=4, alcohol)
Head, W, mm	1.54–1.66	1.53–1.72	1.59–1.69	1.56	1.44–1.64	1.66	1.69	1.57–1.77
Ratio, head W : eye W	1.95–2.17:1	1.94–2.22:1	1.95–2.03:1	1.90:1	1.99–2.23:1	1.79:1	2.23:1	1.62–2.06:1
Dist.between tentoria, mm	0.36–0.50	0.43–0.51	0.45–0.51	0.45	0.43–0.53	0.51	0.50	0.44–0.48 (N=3)
Frons, L, mm	0.44–0.50	0.43–0.52	0.42–0.44	0.47	0.44–0.47	0.48	0.47	0.39–0.46 (N=3)
Clypeus, L, mm	0.22–0.30	0.24–0.29	0.24–0.28	0.26	0.18–0.26	0.27	0.30	0.23–0.26 (N=3)
Antenna, L, mm	10.2 (N=1)	9.2–9.5 (N=3)	9.3–10.3	–	9.4 (N=1)	9.7	–	8.4–11.0 (N=2)
Pronotum, L, mm	0.69–0.73 (N=3)	0.68–0.92	0.71–0.90	0.71	0.63–0.84	0.87	0.91	0.66–0.83
Pronotum, W, mm	1.05–1.14 (N=3)	0.99–1.17	0.98–1.14	1.04	0.92–1.13	1.06	1.21	1.01–1.13 (N=3)
Ratio, pronotum, W:L	1.61–1.70:1 (N=3)	1.65–1.78:1	1.57–1.72:1	0.68:1	0.67–0.75:1	0.8:1	0.75:1	0.73–0.79:1 (N=3)

	Chrysopodes (*N.*) *nigricubitus* s.p. n.		
	Santa Cruz	Santa Cruz	Pinta
	Table Mtn.	Hornemann Farm	420 m
	(N=4)	(N=3)	(N=2)
Head W, mm	1.59–1.69	1.46–1.59	1.39–1.45
Ratio, head W : eye W	2.17–2.48:1	2.26–2.51:1	2.68:1
Dist.between tentoria, mm	0.47–0.54	0.46–0.52	0.44–0.49
Dist. between antennae, mm	0.09–0.12	0.10–0.11	0.12
Frons L, mm	0.44–0.59	0.44–0.51	0.42–0.44
Clypeus L, mm	0.29–0.33	0.27–0.30	0.27–0.32
Antenna L, mm	8.2–9.6 (N=3)	9.2–9.3 (N=2)	10.1 (N=1)
Pronotum L, mm	1.02–1.35	0.95–1.14	0.88
Pronotum W, mm	1.16–1.56	1.06–1.17	1.00
Ratio, pronotum W : L	0.85–0.93:1	0.90–1.01:1	0.88:1

Figure 5. Base of forewing. **a** *Chrysopodes* (*Neosuarius*) *nigripilosus* **b** *C.* (*N.*) *nigricubitus* **c** *C.* (*N.*) *pecki*. ***icux2***, second intracubital crossvein; **ma**, median arculus.

[between R and radial sector (Rs)]; height of tallest radial cell about 0.2 times height of wing. Radial sector slightly thickened at intersection with first radial crossvein (rx1). First intramedian cell ovate, length about 3/4 length of third medial cell; median arculus (ma) thickened. Usually two rows of gradate veins; inner row with three to five gradates in irregular pattern; outer row with six to seven, ~regularly stepped gradates (six specimens with three rows – the middle row with one to two gradates). Four b cells, four b' cells; cubitus (Cu) thickened at furcation; three intracubital cells, distal one open, icu1, icu2 each shorter than icu 3; icu1 longer than icu2; second intracubital crossvein (icux2) relatively straight, not thickened, without swellings. First anal vein (1A) forked.

Hindwing narrow, length over three times greater than height, with apex acute. Ten to eleven radial crossveins; three to five inner gradates; six to seven outer gradate veins; three b cells; no t cell; four b' cells; two intracubital cells, distal one open.

Forewing hyaline, with stigma slightly opaque; costal veinlets within stigma brown, surrounded with suffusion of light brown. Alar membrane almost completely without suffusion of colored pigment. Longitudinal veins cream-colored, marked with dark brown to black at intersections with crossveins. Most costal veinlets, almost all crossveins cream-colored in center, dark brown at tips. Gradates dark brown to black; terminal veinlets dark brown basally, brown at tips, with cream-colored sections mesally. Rs black at intersection with Rx1; ma black; Cu black at furcation; marginal cell below 3A almost completely dark brown to black. Hindwing hyaline; membrane without suffusion of colored pigment; stigma opaque, brownish. Longitudinal veins cream-colored, marked with dark brown at intersections with crossveins; gradates, icu crossvein dark brown; costal veinlets, most crossveins dark brown at tips, cream-colored in center.

Abdomen (male & female) (Table 5, Fig. 6a, b). Tergite 1 light brown to brown; T2, 3, 6, 7, brown; T4, 5 brown distally; pleural regions cream-colored, mottled with brown; sternites 1–4 cream-colored with cream-colored setae; setae brown on S5–9; Female: S5, S6 brown, S7 brown or brown basally; terminus light to dark brown; Male: S5 to S8+9 cream-colored to tan. Tergites 6, 7: roughly quadrate, with relatively straight ventral margins, straight basal margins, rounded distal margins; length: 1.4–1.5 (T6), 1.1–1.2 (T7) times greater than height (lateral view); with long, robust setae. Pleural region, P7 with dense, medium-length setae. Sternite 6: quadrate, dorsal margin relatively straight; length ~0.8 times height, with long, robust setae. Spiracles oval, not enlarged, ~0.02–0.04 mm diameter; atria not enlarged.

Figure 6. Abdomen, ventral view. **a** *Chrysopodes* (*Neosuarius*) *nigripilosus* male **b** *Chrysopodes* (*Neosuarius*) *nigripilosus* female **c** *C.* (*N.*) *nigricubitus* female **d** *C.* (*N.*) *pecki* female. The scale applies to all images.

Male. (Table 5, Figs 7, 8, 9a, b, c). Eighth tergite (T8) truncate anteriorly, posteriorly (lateral view). Left and right T9+ectoproct fused dorsally; terminal edge rounded dorsally; vertical margin straight, rounded ventrally; vertical field of long, dense, robust setae distally. Apodeme of T9+ectoproct heavily sclerotized, arched, with three terminal branches: dorsal branch extending upward, internally beneath callus cerci, connecting mesally at top of tergite; short ventral branch extending into membrane below apodeme; caudal branch heavy, extending distally well beyond tip of T9+ectoproct, curved mesally, with rounded, forked tip (Fig. 9a). Callus cerci taller than wide (0.17–0.19 mm tall, 0.13 mm wide), with 31–32 trichobothria. S8+9 length 1.6–1.7 times proximal height; shape in lateral view: triangular to slightly truncate distally, with well sclerotized, sub-basal apodeme extending transversely across entire sternite; terminal membrane modified into pair of eversible, elongate pouches, separated by unmodified, flat, mesal membrane. Subanal plate lightly sclerotized, with large patch of long, delicate setae. Gonarcus arcuate, loosely attached to T9+ectoproct via delicate membrane beneath subanal plate; bridge well-sclerotized, broad, flat transversely, with gonarcal arms extending downward from distal margins of bridge; span of gonarcus near arch 0.31–0.32 mm, span between gonarcal arms distally 0.37–0.46 mm. Gonarcal arms oblong, ~0.32–0.36 mm long. Mediuncus lightly sclerotized, broad basally, more heavily sclerotized, cone-shaped, distally, slightly rounded dorsally; base broadly attached and extending from top of gonarcus, with pair of elongate, internal rods extending along dorsal margin of mediuncus from base to well past middle of mediuncus. Sclerotized surface of mediuncus rough, with very fine striations above, minute microsetae laterally. Tip of mediuncus bent downward, elongate, tapering to rounded, beak-like apex, with thin, mesal flange above beak. Membrane immediately below beak (base of gonosaccus) bearing pair of long, thin, setose glands with grainy

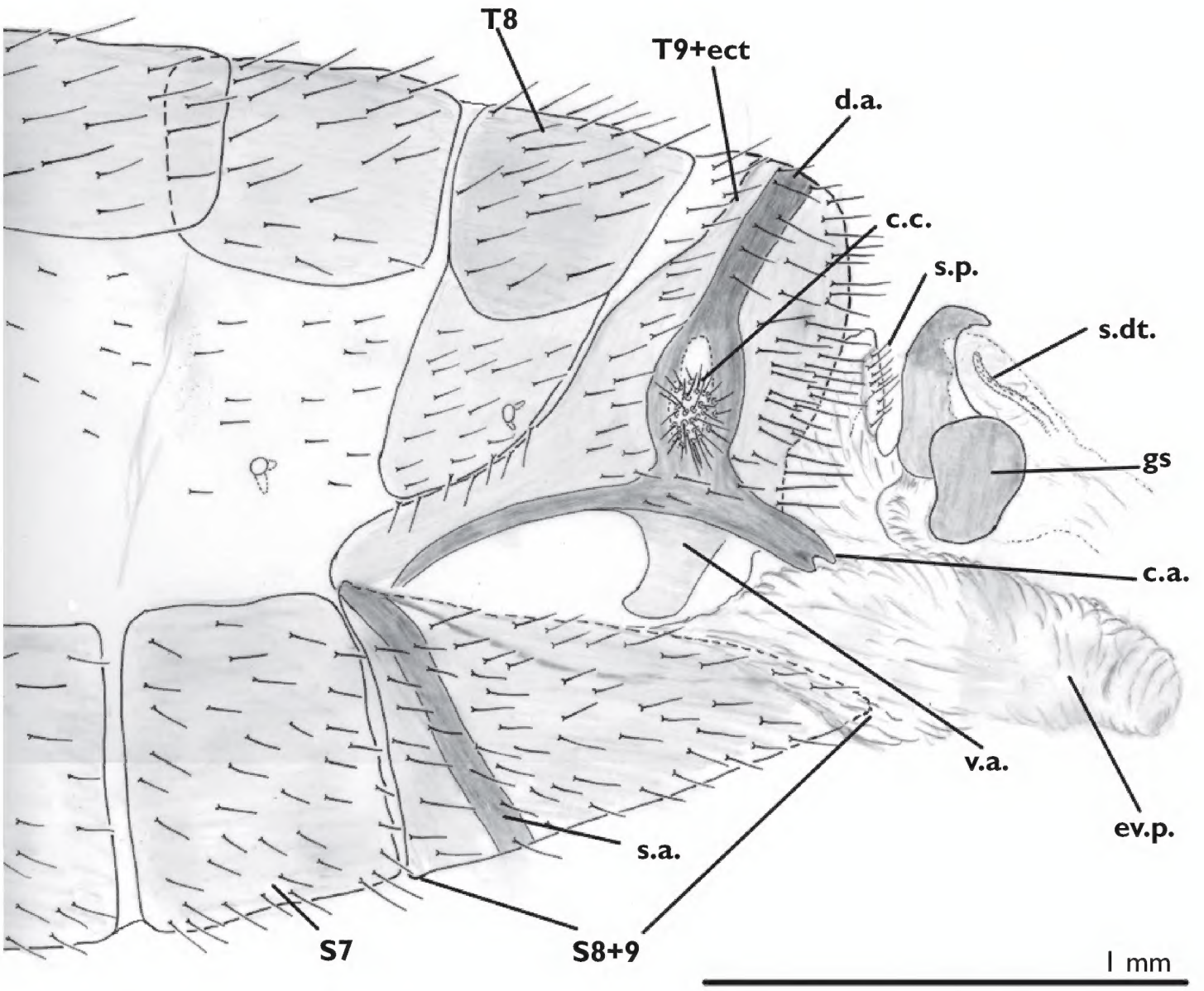


Figure 7. Male abdomen, lateral view. *Chrysopodes* (*Neosuarius*) *nigripilosus*. **c.a.** tip of caudal apodeme on T9+ectoproct **c.c.** callus cerci **d.a.** dorsal apodeme on T9+ectoproct **ev.p.** eversible membranous pouch **gs** gonarcus (lateral apodeme) **s.a.** sub-basal apodeme on S8+9 **s.dt.** setose duct **s.p.** setose subrectal plate **S7** seventh sternite **S8+9** fused eighth and ninth sternites **T8** eighth tergite **T9+ect** fused ninth tergite and ectoproct **v.a.** ventrally projecting arm of apodeme on T9+ectoproct.

interior (glands sometimes ribbon-like – probably teneral condition); base of glands sometimes with short, stout setae, sometimes stemming from crescent-shaped sclerotized protuberances; length of glands approximately two times width of gonarcal bridge; terminus of glands apparently merging with gonosaccus membrane well below origin of ducts; gonosaccus membrane distal to gonarcus folded, with rough-textured surface. Hypandrium internum with pair of broad, almost transparent arms, very flat, wing-like comes. Gonapsis absent.

Female (Table 5, Figs 12, 13, 14, 15). Tergite 8: height of fully sclerotized portion approximately equal to length; height of sclerite (including less sclerotized ventral extension) ~two times length, unsclerotized portion with numerous medium-length setae. Ninth tergite + ectoproct (lateral view) very slightly tilted – ventral margin extending slightly beneath T8; proximal margin relatively straight throughout or slightly

Figure 8. Male abdomen, lateral view. *Chrysopodes* (*Neosuarius*) *nigripilosus*. Note pair of eversible pouches at terminus of S8+9.

convex; distal margin curving beneath ventral margin of gonapophyses laterales (mature specimens). Callus cerci taller than broad (0.16–0.17 mm tall, 0.10–0.14 mm wide), with ~31–36 trichobothria. Gonapophyses laterales 0.4–0.5 times height of T9+ectoproct; ~2.6–4.7 times taller than wide; with robust setae dorsally, shorter, thinner setae ventrally; rounded dorsally, ventrally; orientated posteroventrally (~60–70° angle from midline). Sternite 7: with long, robust setae; length ~1.6 times height of proximal margin (lateral view), with distal 1/4 sloping abruptly to terminus; terminus almost as tall as midpoint of segment. Subgenitale narrow, rounded, with broad, bilobed, distal process; base consisting of light, folded membrane, attached to S7 via delicate, invaginated membrane; lateral margin of base with pair of small, flat pouches, near but separate from base of bursal glands; pouches ~1/6 length of spermatheca. Pair of large, bulbous bursal glands with narrow, elongate ducts opening on dorsolateral margin of bursa (ducts possibly with small setae or scales), with broad, elongate, sometimes branched, accessory ducts distally. Bursa narrow (< 1/2 width of segment), but completely covering spermatheca; membrane heavier basally than distally, dorsum with longitudinal folds, opening ventrally to bursal duct. Bursal duct broadly fluted, transversely folded, immediately below bursa. [The origin of the fluted area below the bursa is not completely clear. We consider it to be an enlarged part of the bursal duct and label it as such on the figures. However, we recognize that it could be part of the bursa copulatrix, in which case the bursal duct would be greatly reduced.] Spermatheca elongate, tubular, with distal end slightly bulbous, one bend, after midsection (to

the right), open to bursa via elongate dorsal slit throughout; 0.12 mm diameter at mouth (distal end), 0.18 mm diameter in midsection (widest area), 0.5–0.6 mm long; invagination oblong, extending ~1/2 length of spermatheca (length 0.23–0.25 mm); velum not identified. Spermathecal duct short, not well sclerotized at tip, ~0.65 mm long (not including pale, brushy tip), extending from slit on dorsal margin of spermatheca, curving, entering subgenitale, making U-shaped curve along dorsal surface of subgenitale cavity, then looping in front of spermatheca; distal ¼ brushy. Colleterial gland elongate, narrow, extending slightly into A6, with smooth, untextured surface, base with bulbous, folded reservoir near terminus of duct; no accessory glands found. Transverse sclerification curved, eliptoid, plate-like, located mesally within gonopophyses laterales, with two rows of setae (setae longer mesally than laterally).

Intraspecific variation. See measurements (Tables 1, 3).

Baltra. The lectotype (AMNH) is teneral. It has a mediuncus that is characteristic of mature specimens, but the gonarcal arms are barely formed, the glandular ducts are visible only in a small region at the base of the gonarcal arms, and the eversible pouches are small and withdrawn. The dissected paralectotype (MCZ) is mature, with structures as described above.

Santa Cruz (Academy Bay). The large series of specimens from this locality are relatively uniform, and in all the features that we measured, they overlap with those from the type locality. Although they tend to have somewhat longer wings (Table 3), their head size and proportions, as well as the features of the wings, are well within the range of the Baltra specimens (Tables 1, 3).

The dorsal surface of specimens from Academy Bay is relatively dark (light brown to brown); the lateral and ventral surfaces of the thorax are light brown to tan; dorsally the abdomen is cream-colored to light brown, with areas marked with brown; ventrally the abdomen is cream-colored to light tan (entirely in the males; with S5, S6 and S7 brown in the females). The facial markings range from medium depth to dark. The membrane of the wings is without markings or suffusion; the degree to which the Rs, ma and Cu are thickened is small; and there are three to four crossveins below the stigma. In the four dissected males, (a) the gonarcal arms are oriented downward; (b) the eversible pounches are large and well separated. [Note: One of the ~65 specimens has a small amount of suffusion around the gradates and some crossveins, but none of the other characteristics of *C.* (*N.*) *nigricubitus;* four of 65 specimens (from the 1968 Edinbrough University Expedition) have two crossveins below the stigma; of these, two have three crossveins on the opposite wing.]

Isabela. The *C.* (*N.*) *nigripilosus* specimens from Isabela overlap with the Baltra specimens in the features we examined. Among these specimens (both pinned and in alcohol), there were no distinguishing features with regard to head size, head features, or wing size or wing features (See measurements, Tables 1, 3).

The overall body color is tan with mottled, light to medium brown dorsal markings; the ventral abdominal markings of the males and females match those of the Baltra population. The facial markings range from light to medium brown. The membrane of the wings is without markings or suffusion; the degree to which the Rs, ma

and Cu are thickened is small; and there are three to four crossveins below the stigma. On the two dissected male specimens from this island: (a) the gonarcal arms extend downward from the gonarcal bridge, parallel with the mediuncus, and (b) the eversible pouches are short and highly folded; although they are fully separate, the area between them is membranous and loose.

Fernandina. In general, the specimens from this island (2 pinned and 7 in alcohol) overlap with the Baltra specimens. The degree to which the Rs, ma and Cu are thickened is small; the membrane of the forewing is clear and without marks; there are three crossveins below the stigma (Table 3).

Santa Fe, Santiago. The single female specimens from Santa Fe and Santiago Islands have features that are typical of the Baltra population (Tables 1, 3).

Specimens examined (in addition to the type material; all are pinned unless noted otherwise): ***Baltra*** (= South Seymour). South Seymour, IV/23/1923, Williams Galápagos Exped., Dept. of Tropical Research, N. Y. Zoological Society, William Beebe, Director (1M, Lectotype, AMNH); So. Seymour Isl., IV/20/1923, Am. Mus. Exped. (1M, 2F, 1 abdomen missing, Paralectotypes, MCZ); 30 m, S. Peck, I/24/1989, arid zone, grass+Bursera Forest, UV light, 89–4 (2M, USNM); 10 m, I/23/1989, S. Peck, arid zone, Bursera Forest, UV light, 89–5 (1F, USNM), beating or on ground, 89–12 (1M, USNM). ***Santa Cruz*** (= Indefatigable). CDRS, Arid zone, II/5–9/1989, dung tp., B. J. Sinclair (1F, USNM); Academy Bay, II/17/1964, P. D. Ashlock, (1M, 1F, BPBM); 0–100 m IX/1970, J. & M. Sedlacek (2F, BPBM); Academy Bay, Darwin Research Station, I/25-II/27/1964, D. Q. Cavagnaro & R. O. Schuster (3M, 11F, CAS), III/21/1964, D. Q. Cavagnaro (1M, CAS), I/30/-III-20/1964, R. O. Schuster (30M, 13F, CAS), I/21-II/1/1964, E. G. Linsley (2M, 1F CAS); CDRS, X/12–27/1968, Edin. Univ. Exped 1969.71 (4F, 2?, NSM, det. A. R. Waterston, 1970). ***Isabela*** (= Albemarle). nr, Punta Tortuga N, of Tagus Cove, I/28–30/1967, edge of mangrove swamp, among *Bursera graveolens*, I. L. Wiggins (1M, CAS); Puerto Villamil, MVL, III/2/1989, B. Laudry (1M, 1F, USNM); V. Alcedo, arid zone, 200m, Palo Santo woodland uv light, IV/3/1996, S. Peck, 96–78 (1M, 1F, USNM); V. Wolf, summit arid, 1700m, sweeping shrubs, V/21/1996, S. Peck, 96–201 (1F, USNM); Beagle Crater, 3 m. (beach), III/25/1988, 4 m. (beach), III/23/1988, L. Baert, K. Desender & J.-P. Maelfait (6M, 2F, IRSNB, Sample #B.88/0478; alcohol); Volcán Wolf, 4 m. (beach), III/20/1988, L. Baert, K. Desender & J.-P. Maelfait (2M, 5F, IRSNB, Sample #B.88/0446; alcohol); Volcán Wolf, 4 m. (beach), III/23/1988, L. Baert, K. Desender & J.-P. Maelfait (11M, 8F, IRSNB, Sample #B.88/0470; alcohol). ***Fernandina*** (= Narborough). W side, 1,100', II/5/1964, D. Q. Cavagnaro (2F, CAS); Beginning of encañada, V/4/1991, L. Baert, K. Desender & J.-P. Maelfait (1F, IRSNB, Sample #B.91/0765; alcohol); Cabo Hammond, 5 m, V/12/1991, L. Baert, K. Desender & J.-P. Maelfait (4M, 2F, IRSNB, Sample #B.91/0802; alcohol). ***Santa Fe*** (= Barrington). Lagoon, 400 m, IV/24/1991, L. Baert, K. Desender & J.-P. Maelfait (1F, IRSNB, Sample #B.91/0722; alcohol). ***Santiago*** (= San Salvador, James). Settlement, IX/22/1968, Edin. Univ. Exped. 1969.70 (1F, NMS, det. A. R. Waterston 1970).

[Note: Additional specimens from Santa Cruz Island are in the NMS.]

***Chrysopodes (Neosuarius) nigricubitus* sp. n.**
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Diagnosis. *Chrysopodes* (*Neosuarius*) *nigricubitus*, the second species of endemic *Chrysopodes* (*Neosuarius*) to be recognized from the Galápagos Archipelago, currently is known from two islands: Santa Cruz [Table Mountain (440 m) and Horneman Farm (220 m)] and Pinta (west side of island, 420 m). The adults of this species share many features with *C.* (*N.*) *nigripilosus* and *C.* (*N.*) *pecki*: they have small, robust, brownish bodies, brown head and facial markings, relatively narrow wings with a narrow costal area, and cream-colored wing venation marked with black (Figs 1, 2, 4). However, a suite of distinguishing features (external and internal) in both males and females indicates that these specimens represent a distinct species.

The most prominent distinguishing feature of the species is the suffusion of black or dark brown pigment (coloration) around many of the crossveins on the forewings (Figs 4b, 5b). This suffusion is absent from the other two *Chrysopodes* species on the Galápagos Islands. In *C.* (*N.*) *nigricubitus*, the second cubital crossvein bears a distinct, dark brown to black swelling that is absent from *C.* (*N.*) *nigripilosus* and small on *C.* (*N.*) *pecki*. Also, there are consistent differences between the species in the length : width ratios of the pronotum and abdominal tergite 6; for both structures, the *C.* (*N.*) *nigricubitus* ratios are intermediate between those of *C.* (*N.*) *nigripilosus* and *C.* (*N.*) *pecki* (Tables 2, 5). Among the specimens that we studied, there was no overlap between the species in the values of any of these traits. In addition, the abdominal sternites of female *C.* (*N.*) *nigricubitus* are cream-colored to light tan, without dark brown areas like those on the S5-S7 of *C.* (*N.*) *nigripilosus* and *C.* (*N.*) *pecki* females (Fig. 6).

Although the *C.* (*N.*) *nigricubitus* genitalia resemble those of *C.* (*N.*) *nigripilosus* and *C.* (*N.*) *peck,* there are distinguishing features in the *C.* (*N.*) *nigricubitus* males. First, unlike *C.* (*N.*) *nigripilosus* and *C.* (*N.*) *pecki,* in which the lateral arms of gonarcus are directed downward next to the mediuncus, in *C.* (*N.*) *nigricubitus* the gonarcal arms are spread widely (Fig. 10c vs Figs 9c & 11c). Only the tips of the gonarcal arms bend downward, and the gonarcal structure is relatively flat in lateral view. Second, in *C.* (*N.*) *nigricubitus.* the horizonal apodeme along the ventral margin of T9+ectoproct is relatively straight (lateral view), not arched as in *C.* (*N.*) *nigripilosus.* The tip of the caudal branch of the apodeme is pointed and without a flange; whereas in *C.* (*N.*) *nigripilosus* it is forked, with both tips rounded, and with the upper fork having a flange-like membrane attached (Fig. 10a).

In the female genitalia, we detected small, but consistent differences between *C.* (*N.*) *nigricubitus* and the other two Galápagos species. First, the sclerotized portion of the *C.* (*N.*) *nigricubitus* spermathecal duct tends to be slightly shorter than that of *C.* (*N.*) *nigripilosus* (0.65 vs. 0.40 mm) (Table 5). Second, the tip of the distal knob of subgenitale is slightly more elongate than that on the two other species, and, third, the pouches near the base of the bursal glands are flat and folded as in *C.* (*N.*) *nigripilosus* but not *C.* (*N.*) *pecki* (Compare Fig. 15b with 15a, 15c).

Table 2. Range of variation in head and thoracic features among three *Chrysopodes* (*Neosuarius*) species from the Galápagos Islands.

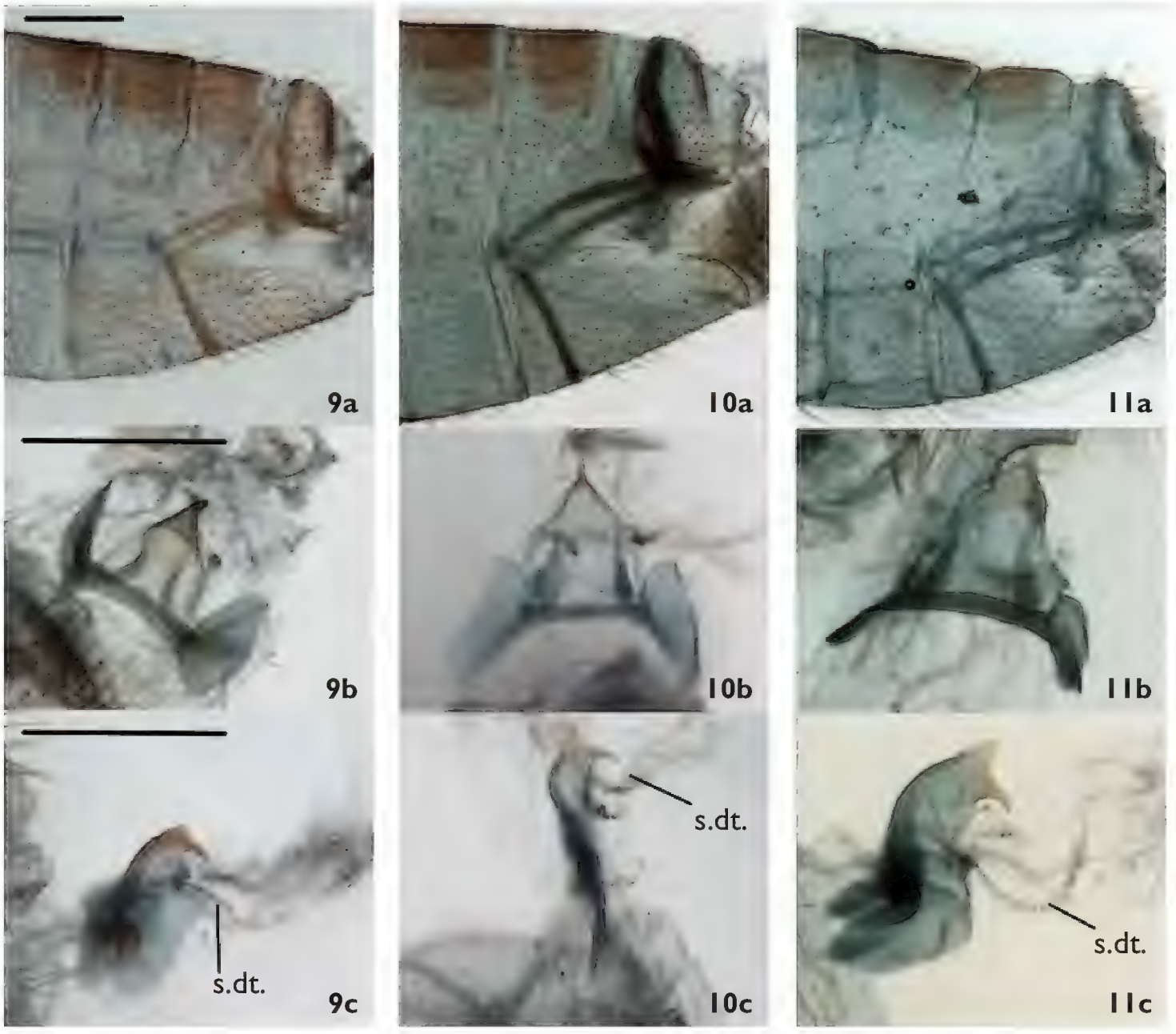
	C. (*N.*) *nigripilosus* (Banks)	*C.* (*N.*) *nigricubitus* sp. n.	*Chrysopodes* (*N.*) *pecki* sp. n.
	8 localities, 5 islands†	3 localities, 2 islands‡	2 localities, 1 island§
	N=21	N=7	N=3
Head W, mm	1.44–1.72 (N=21)	1.39–1.69 (N=9)	1.57–1.68, 1.43
Ratio, head W : eye W	1.79–2.23:1 (N=21)	2.17–2.68:1 (N=9)	2.35–2.55, 2.58
Dist.between tentoria, mm	0.43–0.53 (N=20)	0.44–0.54 (N=9)	0.52–0.53, 0.44
Frons L, mm	0.42–0.48 (N=20)	0.42–0.59 (N=9)	0.53–0.56, 0.51
Clypeus L, mm	0.18–0.30 (N=20)	0.27–0.33 (N=9)	0.23–0.29, 0.24
Antenna L, mm	9.2–10.3 (N=10)	8.2–10.1 (N=6)	–
Pronotum L, mm	0.63–0.92 (N=19)	0.88–1.35 (N=9)	1.25–1.30, –
Pronotum W, mm	0.92–1.21 (N=18)	1.00–1.56 (N=9)	1.14–1.20, –
Ratio, pronotum W : L	0.61–0.8:1 (N=18)	0.85–1.01:1 (N=9)	1.09–1.10:1, –

† Baltra (no specifics), Santa Cruz (Academy Bay), Isabela (Puerto Villamil, Punta Tortuga, Volcán Wolf, Volcán Alcedo), Santa Fe (lagoon), Fernandina (Cabo Hammond)
‡ Santa Cruz (Table Mtn., Hornemann Farm), Pinta (420 m)
§ Isabela (Volcán Wolf, Volcán Alcedo; N=2F, 1M)

Description. All features are as described for *C.* (*N.*) *nigripilosus* except as follows. *Head* (Table 2, Fig. 2): Vertex: surface with small, amber setae. Labrum: distal margin with slight mesal cleft. *Coloration.* Head cream-colored frontally, tan to light brown dorsally, with brown streak lateral to eyes; frons with pair of oblong, brown marks below most of lower margin of torulus; clypeus with lateral margins dark brown; toruli cream-colored to light tan, with brown border surrounding sclerotized margins; dorsal torulus with dark brown, vertical streak. Genae dark brown ventrally, white stripe above, dark brown dorsally. Scapes tan, unmarked; pedicel tan to light brown; flagellum light brown. Maxillary palp: basal two segments cream-colored. Venter: lateral margins of submentum cream-colored to tan.

Thorax (Table 2, Fig. 2b). Pronotum approximately same width as length; with mottled light brown markings. Mesonotum: with setae short, delicate, amber. Pleural areas: cream-colored, without markings. Legs: setae amber.

Wings (Table 4, Figs 4b, 5b). Costal area: greatest height ~0.16–18 times height of wing; tallest at costal cell (#4–6). Subcosta: two subcostal crossveins below stigma. Nine to eleven radial crossveins (between R and Rs); ma considerably more thickened than the Rs at rx1; two rows of gradates; inner row with three to four gradates, outer row with five to six, both rows in regular pattern. Cubitus thickened near furcation; icux2 curved, with dark brown, bubble-like expansion mesally.



Figures 9–11. Male terminal structures. **9** *Chrysopodes* (*Neosuarius*) *nigripilosus* **10** *C.* (*N.*) *nigricubitus* **11** *C.* (*N.*) *pecki* **a** terminal segments of abdomen, lateral view (scale = 0.5 mm, all images in row) **b** gonarcus, dorsal view (scale = 0.1 mm, all images in row) **c** gonarcus, lateral view (scale = 0.1 mm, all images in row). **s.dt.**, setose duct. Note : The gonarcal arms of *C.* (*N.*) *nigripilosus* (Fig 9b) are unnaturally splayed here by the coverslip ; the tips typically are below the edge of the gonarcal bridge

Hindwing: length approximately three times height. Nine to eleven radial crossveins; three to four inner gradates; five to six outer gradate veins; three b cells; t cell usually present.

Forewing: alar surface surrounding many crossveins with suffusion of brown to dark brown. Stigma very slightly opaque; costal veinlets within stigma brown to black. Base of Rs, rx1 dark brown to black; icux2 dark brown to black, with dark brown, bubble-like swelling mesally. Hindwing: stigma very slightly opaque; veinlets within stigma, dark brown, with dark brown pigment in surrounding area; gradates, icux2 cream-colored to light brown.

Abdomen (male & female) (Table 5, Figs 6, 10). Sternites cream-colored with cream-colored setae, without brown areas. Tergites 6, 7: length: 2.1–2.2 (T6), 1.2–1.9 (T7) times greater than height (lateral view). Spiracles ~0.04–0.05 mm diameter.

Table 3. Range of variation in wing characteristics among geographic populations of two *Chrysopodes* (*Neosuarius*) species from the Galápagos Islands.

	Chrysopodes (*Neosuarius*) *nigripilosus* (Banks)						
	Baltra	Santa Cruz	Isabela	Isabela	Santa Fe	Fernandina	Santiago
	Type locality	Academy Bay	misc†	Beagle Crater	5 m. Lagoon	Cabo Hammond	Settlement
	(N=4)	(N=3)	(N=3)	(N=2, alcohol)	(N=1, alcohol)	(N=3, alcohol)	(N=2, image)
Forewing L, mm	10.6–11.4	11.7–12.2	10.6–12.9	10.2–11.6	11.3	11.6–12.2	–
Ratio, forewing, L:W	2.95–3.13:1	2.94–3.03:1	2.82–3.03:1	2.96–2.97	2.83	2.93–3.01	–
Sc crossveins (below stigma), n	3–4	2–4	3–4	3–4	3	2–4	3
Tallest costal cell, cell #	5–6	5–7	5	5–7	5	5–6	
Ratio, tallest costal cell H : wing W	0.17–0.19:1	0.16–0.18:1	0.17–0.18:1	0.16–0.18:1	0.18	0.16–0.17	
Radial cells, n	10–12	11	11–12	11	11	11–12	11
Ratio, tallest radial cell L: wing W	0.19–0.22:1	0.19–0.21:1	0.19–0.20:1	0.19–0.21:1	0.20:1	0.20:1	
Ratio, im1 W: m3 W	0.67–0.77:1	0.71–0.85:1	0.42–0.73:1	0.72–0.74:1	0.77:1	0.69–0.75	
Inner gradates, n	3–5	4–5	4–5	4–5	6	4–5	5
Outer gradates, n	7	6–7	7–8	7	7	6–7	7
Gradate cell #2, H, mm	1.05–1.72	1.15–1.63	1.01–1.28	0.91–1.13	1.04	1.21–1.50	
Ratio, gradate cell #2, H : W	2.43–3.16:1	2.78–3.86:1	2.69–2.91:1	2.31–2.65	2.46:1	2.79–3.46:1	
Gradate cell #3, H, mm	0.88–1.61	1.55–1.63	1.11–1.43	1.16–1.31	1.37	0.82–1.67	
Ratio, gradate cell #3, H : W	2.07–4.37:1	4.09–4.26:1	3.13–3.83:1	3.33–3.39:1	3.52:1	2.06–4.26:1	
Hindwing L, mm	9.7–10.0 (N=3)	10.3–11.0	9.7–11.5	9.1–10.5	10.0	10.4–10.9	
Ratio, hindwing L : W	3.23–3.50:1 (N=3)	3.09–3.20:1	3.00–3.23:1	3.09–3.15:1	3.07:1	3.03–3.45:1	
Radial cells, n	10–11	11	11–12	11	11	11–12	11–12
Inner gradates, n	3–5	1–4	1–2	3–4	3	3	4

Outer gradates, n	6–7	6–7	6–7	6–7	6	6–7	7
Vein width – crassate veins							
ma W, mm	0. 045–0.050 (N=2)	0.042–0.056	0.038–0.056	0.044–0.048	0.064	0.048–0.064	
Rs at rx1, W, mm	0.051–0.057 (N=2)	0.058–0.076	0.048–0.053	0.054–0.055	0.066	0.054–0.062	
Cu at Cuf, W, mm	0.093–0.094 (N=2)	0.071–0.106	0.081–0.099	0.077–0.102	0.110	0.09–0.12	
icu2 W, mm	0.027–0.029 (N=2)	0.024–0.032	0.022–0.027	0.023–0.026	0.024	0.026–0.032	

	Chrysopodes (*Neosuarius*) *nigricubitus*, n. sp.		
	Santa Cruz	Santa Cruz	Pinta
	Table Mtn.	Hornemann Farm	420 m
	(N=3)	(N=3)	(N=3)
Forewing L, mm	11.8–12.0	11.8–12.8	11.9–12.6
Ratio, forewing, L : W	2.92–3.05:1	3.00–3.12:1	2.92–3.00:1
Subcostal crossveins (below stigma), n	2	2	2
Tallest costal cell, cell #	4–6	5	5–6
Ratio, tallest costal cell H : wing W	0.16–0.17	0.17–0.18:1	0.17–0.18:1
Radial cells, n	9–10	9–10	10–11
Ratio, tallest radial cell H : wing W	0.21–0.22:1	0.21–0.22:1	0.19–0.21:1
Ratio, im1 W : m3 W	0.68–0.77:1	0.63–0.77	0.72–0.78:1
Inner gradates, n	3	3–4	4
Outer gradates, n	5–6	5–6	6
Gradate cell #2, H, mm	1.23–1.53	1.50–1.93	1.34–1.54
Ratio, gradate cell #2, H : W	2.99–3.29:1	2.93–3.94:1	2.87–3.23:1
Gradate cell #3, H, mm	1.29–1.61	1.54–2.13	1.48–1.65
Ratio, gradate cell #3, H : W	2.71–3.75:1	3.43–4.68:1	3.56–3.76:1
Hindwing L, mm	10.6–10.9	10.6–11.5	10.7–10.8
Ratio, hindwing L : W	3.08–3.19:1	3.07–3.13:1	3.11–3.13:1

Radial cells, n	9–10	10–11	10–11
Inner gradates, n	3	3–4	4
Outer gradates, n	5	5–6	6
Vein width – crassate veins			
ma W, mm	0.089–0.095	0.065–0.114	0.067–0.114
Rs at rx1, W, mm	0.047–0.053	0.051–0.066	0.051–0.054
Cu at Cuf, W, mm	0.076–0.088	0.074–0.187	0.094–0.108
icu2 W, mm	0.091–0.128	0.155–0.165	0.175–0.229

† Punta Tortuga, Puerto Villamil

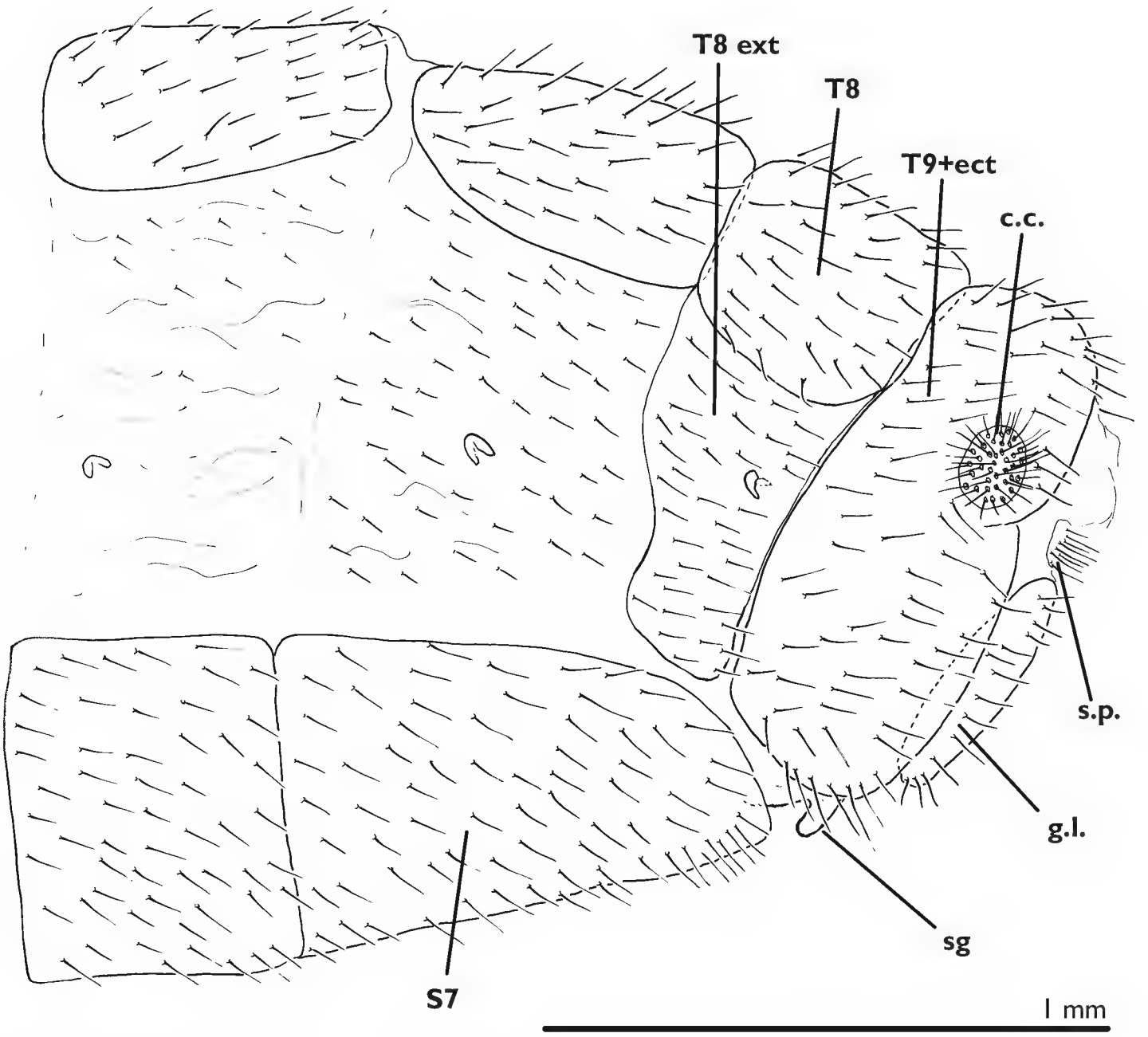


Figure 12. Female terminus, exterior, lateral view. *Chrysopodes* (*Neosuarius*) *nigripilosus*. **c.c.** callus cerci **g.l.** gonapophysis lateralis **sg** subgenitale **s.p.** setose subrectal plate **S7** seventh sternite **T8** eighth tergite **T8 ext**, ventral extension of eighth tergite **T9+ect** fused ninth tergite and ectoproct.

Male. (Table 5, Fig. 10): Apodeme of T9+ectoproct straight to very slightly arched; ventral branch lightly sclerotized; caudal branch acute unforked tip (Fig. 10a). Callus cerci taller than wide (0.15–0.23 mm tall, 0.13–0.18 mm wide), with 34–37 trichobothria. S8+9 length 1.5–1.8 times proximal height; shape in lateral view: triangular, tapering to relatively acute apex. Gonarcus: gonarcal arms extending outward from distal margins of bridge; span of gonarcus near arch 0.27–0.35 mm, span between gonarcal apodemes distally 0.64–0.68 mm. Gonarcal apodemes long, narrow, ~0.32–0.37 mm long. Mediuncus: sclerotized surface smooth, with some microsetae laterally; membrane immediately below beak (base of gonosaccus) with large patch of microsetae or gonocristae surrounding base of setose glands.

Female [Table 5, Fig. 15b; see *C.* (*N.*) *nigripilosus*, Figs 12, 13, 14]. Tergite 8: height of fully sclerotized portion less than length of sclerite; height of sclerite (including less sclerotized ventral extension) ~1.4–1.6 times length. Ninth tergite + ectoproct

(lateral view): distal margin with dorsal and ventral bulges. Callus cerci taller than broad (0.15–0.19 mm tall, 0.14–0.15 mm wide), with ~28–32 trichobothria. Gonapophyses laterales ~0.4 times height of T9+ectoproct; ~2.9–3.3 times taller than wide. Sternite 7: length ~1.6–1.7 times height of proximal margin (lateral view). Subgenitale narrow, rounded, with broad, tongue-like process distally; base consisting of transversely folded, uninvaginated membrane; lateral margin with pair of small, flat pouches, near but separate from base of bursal glands; pouches ~1/3 length of spermatheca. Bursal glands: accessory ducts not observed to be branched distally. Spermatheca: 0.10 mm diameter at mouth (distal end), 0.18 mm diameter in midsection (widest area), 0.5–0.6 mm long; invagination oblong, extending ~1/2 length of spermatheca (length 0.23–0.25 mm). Spermathecal duct: ~0.4 mm long (not including pale, brushy tip).

Type material. The holotype (a male) is in the California Academy of Sciences Collection, San Francisco, CA. It is from a series of specimens collected in 1964 by David Q. Cavagnaro during an Academy expedition to the Galápagos. The type locality is Ecuador, Galápagos Archipelago, Isla Santa Cruz, Table Mountain, 440 meters. The labels on the holotype read: (1) Galápagos Arch. / Isla SantaCruz / Table Mtn. 440 M. / IV-16-1964; (2) D. Q. Cavagnaro / Collector; (3) HOLOTYPE / *Chrysopodes* (*Neosuarius*) *nigricubitus* Tauber & Tauber, des. 2010 [red]. Good condition; glued to point. Altogether, there are 27 paratypes, including thirteen (3M, 8F, 2 teneral, sex undetermined) with identical collection data and yellow paratype labels. Five other paratypes (3M, 2F) have the following data: (1) Galápagos Arch. / Isla SantaCruz / HornemanFarm / 220M V-7-1964; (2) D. Q. Cavagnaro / Collector; (3) PARATYPE / *Chrysopodes* (*Neosuarius*) *nigricubitus* Tauber & Tauber, des. 2010 [yellow]. Nine paratypes (4M, 5F) are in the Institut royal des Sciences naturelles de Belgique, Bruxelles; these specimens are in alcohol, and their printed labels read: (1) Ecuador, Galápagos, Pinta, western side of island, 420 m, 30/II/2000, L. Baert, K. Desender & J.-P. Maelfait, B.00/0100; (2) PARATYPE / *Chrysopodes* (*Neosuarius*) *nigricubitus* Tauber & Tauber, des. 2010.

Etymology. The name, *nigricubitus*, calls attention to one of the species' most prominent distinguishing features – the dark brown to black, heavily sclerotized, second intracubital crossvein [*nigri-* (Latin, prefix), *cubitus* (Latin, noun, masculine)].

Specimens examined. Type material only.

Intraspecific variation. The variation among the specimens we studied is small. See Tables 1, 3 & 5, for the ranges in head size and wing features. One male in the series from Pinta has particularly weakly pigmented wings and genitalia intermediate between *C.* (*N.*) *nigripilosus* and *C.* (*N.*) *nigricubitus*.

Chrysopodes (Neosuarius) pecki sp. n.

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Diagnosis. *Chrysopodes* (*Neosuarius*) *pecki*, the third endemic species of *Chrysopodes* (*Neosuarius*) from the Galápagos, is known from two localities on Isabela Island – Volcán Wolf and Volcán Alcedo, where it is sympatric with *C.* (*N.*) *nigripilosus*. Although

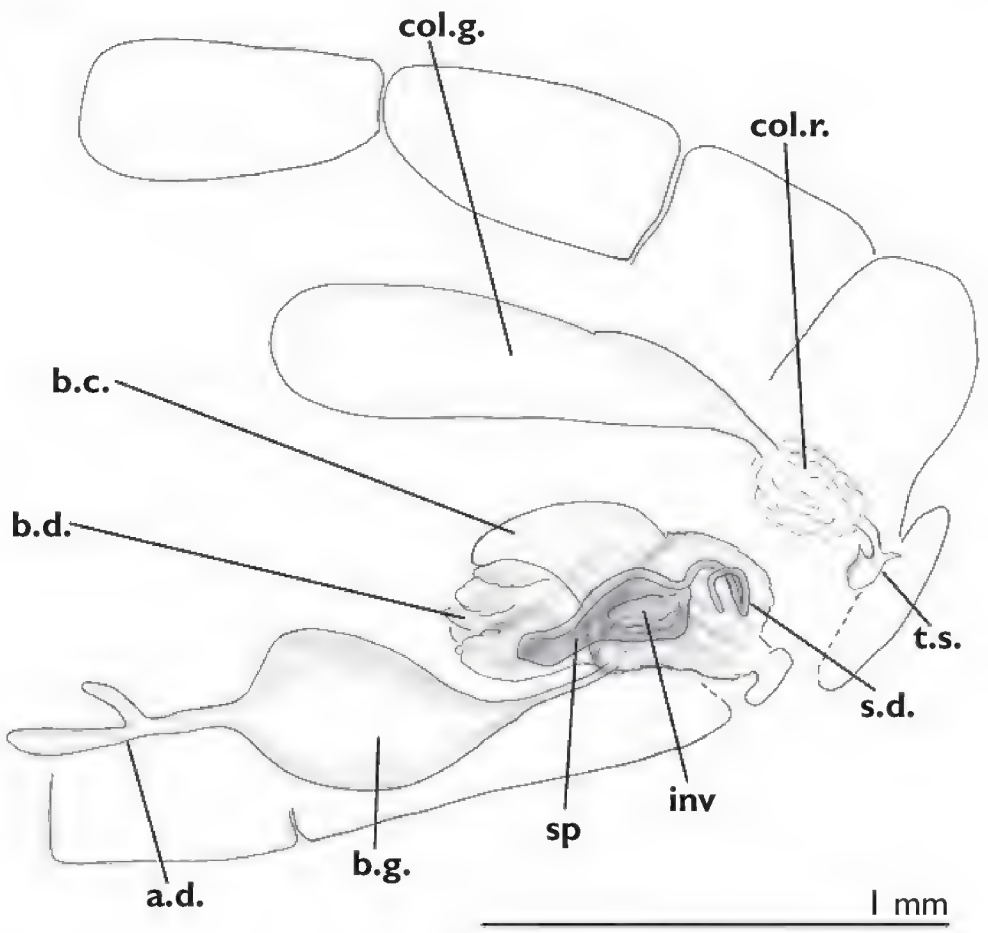

Figure 13. Female terminus, internal, lateral view. *Chrysopodes* (*Neosuarius*) *nigripilosus*. **a.d.** accessory duct on bursal gland **b.c.** bursal copulatrix **b.d.** bursal duct (presumed) **b.g.** bursal gland **col.g.** colleterial gland **col. r.** colleterial reservoir **inv** invagination **sp** spermatheca **s.d.** spermathecal duct **t.s.** transverse sclerification.

the number of specimens that are available is small (N=3) and they share many external and internal features with *C.* (*N.*) *nigripilosus* and *C.* (*N.*) *nigricubitus*, their distinctive size and other features lead us to assign them to a new species.

The most prominent external features of *C.* (*N.*) *pecki* that are absent from the other two Galápagos species include: (a) a pair of brown spots on the dorsum of the head, posterolateral to the vertex (Fig. 3b) and (b) distinctive markings on the venter of the female abdomen (Fig. 6d). On the *C.* (*N.*) *pecki* females, S5 is dark brown, S6 has light brown pigmentation basally, and the distal portion of S6 and all of S7 are cream-colored. In comparison, *C.* (*N.*) *nigripilosus* females have dark brown pigmentation throughout S5, S6, and the base of S7, and *C.* (*N.*) *nigricubitus* females are without dark brown marks on the sternites. *C.* (*N.*) *pecki* is the only one of the three Galápagos species that has wings exceeding 13 mm in length. Like those of *C.* (*N.*) *nigripilosus*, the *C.* (*N.*) *pecki* wings do not show dark suffusion around the crossveins, but like *C.* (*N.*) *nigricubitus,* the second cubital crossvein is very dark and the center of the vein bears a dark brown swelling. In all three *C.* (*N.*) *pecki* specimens, the swelling tends to be smaller than that of *C.* (*N.*) *nigricubitus* (Table 4, Fig. 5c).

C. (*N.*) *pecki* adults may also be characterized by an elongated pronotum. Both female specimens (preserved in alcohol) have a pronotum that is longer than that on *C.* (*N.*) *nigripilosus* (Table 2), and the *C.* (*N.*) *pecki* pronotal length : width ratio is

Table 4. Range of variation in wing characteristics among three *Chrysopodes* (*Neosuarius*) species from the Galápagos Islands.

	C. (*N.*) *nigripilosus* (Banks)	*C.* (*N.*) *nigricubitus* sp. n.	*Chrysopodes* (*N.*) *pecki* sp. n.
	8 localities, 5 islands†	3 localities, 2 islands‡	2 localities, 1 island§
	N=18	N=9	N=2
Forewing L, mm	10.2–12.9 (N=16)	11.8–12.8	13.0–13.7
Ratio, forewing, L : W	2.82–3.13:1 (N=16)	2.92–3.12:1	2.89:1 (N=1)
Subcostal crossveins (below stigma), n	2–4	2	2
Tallest costal cell, cell #	5–7	4–6	4–5
Ratio, tallest costal cell H: wing W	0.16–0.19 (N=16)	0.16–0.18:1	0.17:1 (N=1)
Radial cells, n	11–12	9–11	10
Ratio, tallest radial cell H : wing W	0.19–0.22 (N=16)	0.19–0.22:1	0.21 (N=1)
Ratio, im1 W : m3 W	0.42–0.85:1 (N=16)	0.63–0.78:1	0.70–0.81:1
Inner gradates, n	3–6	3–4	4 (N=1)
Outer gradates, n	6–8	5–6	6 (N=1
Gradate cell #2, H, mm	0.91–1.72 (N=16)	1.23–1.93	1.54 (N=1)
Ratio, gradate cell #2, H : W	2.31–3.86:1 (N=16)	2.87–3.94:1	2.93:1 (N=1)
Gradate cell #3, H, mm	0.82–1.67:1 (N=16)	1.29–2.13	1.69 (N=1)
Ratio, gradate cell #3, H : W	3.13–4.26:1	2.71–4.69:1	3.45:1 (N=1)
Hindwing L, mm	9.1–11.5 (N=165)	10.6–11.5	11.8 (N=1)
Ratio, hindwing L : W	3.00–3.45:1	3.07–3.19:1	3.02 (N=1
Radial cells, n	11–12	9–11	10
Inner gradates, n	1–4	3–4	4
Outer gradates, n	6–7	5–6	6
Vein width – crassate veins			
ma W, mm	0.038–0.064 (N=14)	0.067–0.114	0.051–0.84
Rs at rx1, W, mm	0.048–0.076 (N=14)	0.047–0.066	0.051–0.054
Cu at Cuf, W, mm	0.077–0.120 (N=14)	0.074–0.094	0.054–0.088
icu2 W, mm	0.022–0.032 (N=14)	0.091–0.229	0.054–0.111

† Baltra, Santa Cruz (Academy Bay), Isabela (Puerto Villamil, Punta Tortuga, Volcán Wolf, Volcán Alcedo), Santa Fe (lagoon), Fernandina (Cabo Hammond), Santiago Settlement
‡ Santa Cruz (Table Mtn., Hornemann Farm), Pinta (420 m)
§ Isabela (Volcán Wolf, Volcán Alcedo)

greater than that of either *C.* (*N.*) *nigripilosus* or *C.* (*N.*) *nigricubitus*. The pronotum of the single male specimen (pinned) is distorted and compressed below the mesothorax; its length cannot be measured readily. However, we estimated the length from a lateral view, and it appears to be about as long as those on the female specimens

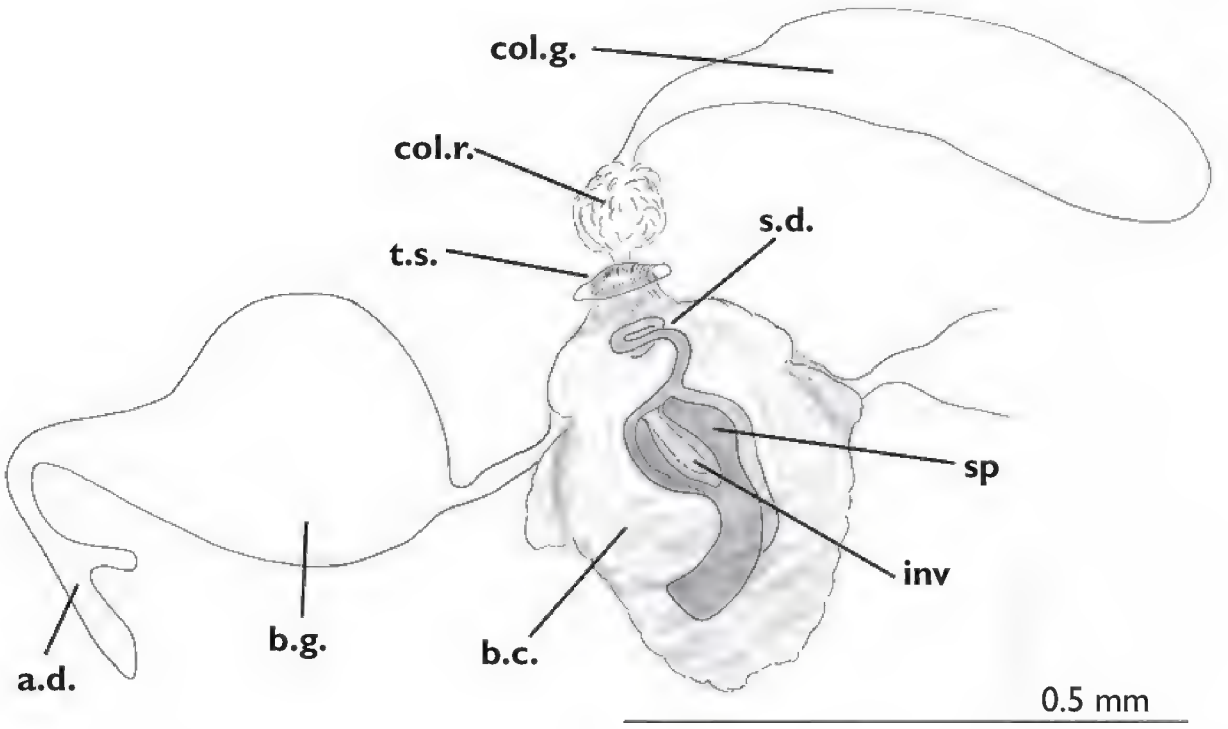

Figure 14. Female, internal reproductive structures, dorsal view. *Chrysopodes* (*Neosuarius*) *nigripilosus*. **a.d.** accessory duct on bursal gland **b.c.** bursa copulatrix **b.g.** bursal gland **col.g.** colleterial gland **col.r.** colleterial reservoir **inv** invagination **sp** spermatheca **s.d.** spermathecal duct **t.s.** transverse sclerification.

C. (*N.*) *pecki* males have abdominal sclerites and genitalia that generally resemble those of *C.* (*N.*) *nigripilosus* and *C.* (*N.*) *nigricubitus* (Fig. 11). However, there are some distinguishing features. First, the size of the gonarcus (length of arms, bridge width) is larger than that of either *C.* (*N.*) *nigripilosus* or *nigricubitus* (Table 5). And, the lateral arms of the gonarcus are directed inward next to the mediuncus as in *C.* (*N.*) *nigripilosus* (Fig. 11b, c). Second, as in *C.* (*N.*) *nigricubitus,* the dorsal apodeme along the ventral margin of T9+ectoproct is relatively straight, and the caudal branch has a well sclerotized, unforked, pointed tip (Fig. 11a). However, in *C.* (*N.*) *pecki* the tip has a small, beak-like flange with a membrane attached (not visible on Fig. 11a). Third, unlike either of the other species, the ventral branch of the dorsal apodeme is elongate, well sclerotized, and angled anteriorly; distally it turns and invaginates within S8+9 (Fig. 11a). And, fourth, although the dorsal apodeme itself is thin (lateral view), the base of the dorsal branch (that extends under the callus cerci) is heavy and densely sclerotized.

In addition to the ventral marks on the abdomen, we detected some other characteristics that distinguish the female terminalia of the *C.* (*N.*) *pecki* specimen we examined. First, the sixth and seventh tergites were slightly longer in actual length, and in their length to height ratio, than those on any of the *C.* (*N.*) *nigripilosus* or *C.* (*N.*) *nigricubitus* specimens (Table 5). Second, as in the two other species, the membrane that is basolateral to the subgenitale bears a pair of invaginated pouches that are near, but separate from, the base of the bursal glands. In *C.* (*N.*) *pecki*, these pouches are clear and bulbous, not flat and folded as in the other two species (Fig. 15c). In all other traits, the female that we measured tended to be large, but the measurements overlapped with those of large *C.* (*N.*) *nigricubitus* specimens.

Table 5. Range of variation in abdominal features among three *Chrysopodes* (*Neosuarius*) species from the Galápagos Islands.

	C. (*N.*) *nigripilosus* (Banks)	*C.* (*N.*) *nigricubitus* n. sp.	*Chrysopodes* (*N.*) *pecki* n. sp.
	8 localities, 5 islands[1]	3 localities, 2 islands[2]	2 localities, 1 island[3]
	(N=3M, 3F)	(N=3M, 3F)	(N=1M, 1F)
MALE & FEMALE			
Abdomen, T6, Ratio, L : H	1.4–1.5:1	2.1–2.2:1	2.3, 3.0:1
Abdomen, T7, Ratio, L : H	1.1–1.2:1	1.2–1.9:1	1.8, 2:1
Abdomen, S6, Ratio, L:H	0.8:1	0.8–0.9:1	1.0, 0.9:1
MALE			
Abdomen, S8+9, Ratio, L : H	1.6–1.7:1	1.5–1.8:1	1.8:1
Callus cerci H, mm	0.17–0.19	0.15–0.23	0.23
Callus cerci W, mm	0.13	0.13–0.18	0.16
Trichobothria, n	31–32	36–37	30
Gonarcal apodemes, basal span, mm	0.31–0.32	0.27–0.34	0.39
Gonarcal apodemes, distal span, mm	0.37–0.46	0.77–0.79	0.57
Gonarcal apodemes, L, mm	0.32–0.36	0.32–0.37	0.39
FEMALE			
Abdomen, S7, Ratio, L : H	1.6:1	1.6–1.7:1	1.6:1
Callus cerci H, mm	0.16–0.17	0.15–0.19	0.19
Callus cerci W, mm	0.10–0.14	0.14–0.15	0.17
Trichobothria, n	31–36	28–32	35
Spermatheca L, mm	0.5–0.6	0.5–0.6	0.6
Spermatheca diameter (at mouth), mm	0.12	0.10	0.13
Spermatheca diameter (widest), mm	0.18	0.16	0.19
Spermathecal duct (sclerotized portion) L, mm	~0.65	~0.40	~0.70

[1] Baltra, Santa Cruz (Academy Bay), Isabela (Puerto Villamil, Punta Tortuga, Volcán Wolf, Volcán Alcedo), Santa Fe (lagoon), Fernandina (Cabo Hammond)
[2] Santa Cruz (Table Mtn., Hornemann Farm), Pinta (420 m)
[3] Isabela (Volcán Wolf, Volcán Alcedo)

Description. All features as in *C.* (*N.*) *nigripilosus* except as noted below. *Head* (Table 2; Fig. 3). Vertex: surface with small, amber setae. Labrum: distal margin with slight mesal cleft. *Coloration.* Head cream-colored frontally, lateral to eyes, tan dorsally; frons with pair of triangular to bowl-shaped, dark brown marks below torulus; clypeus with lateral margins dark tan, dark brown streak extending dorsolaterally from distal margin of tentorial pits almost to eye; toruli cream-colored, with light tan border surrounding sclerotized margins; dorsal torulus with or without grape-brown, vertical streak. Genae cream-colored with dark brown on ventral margin, dark brown dorsally.

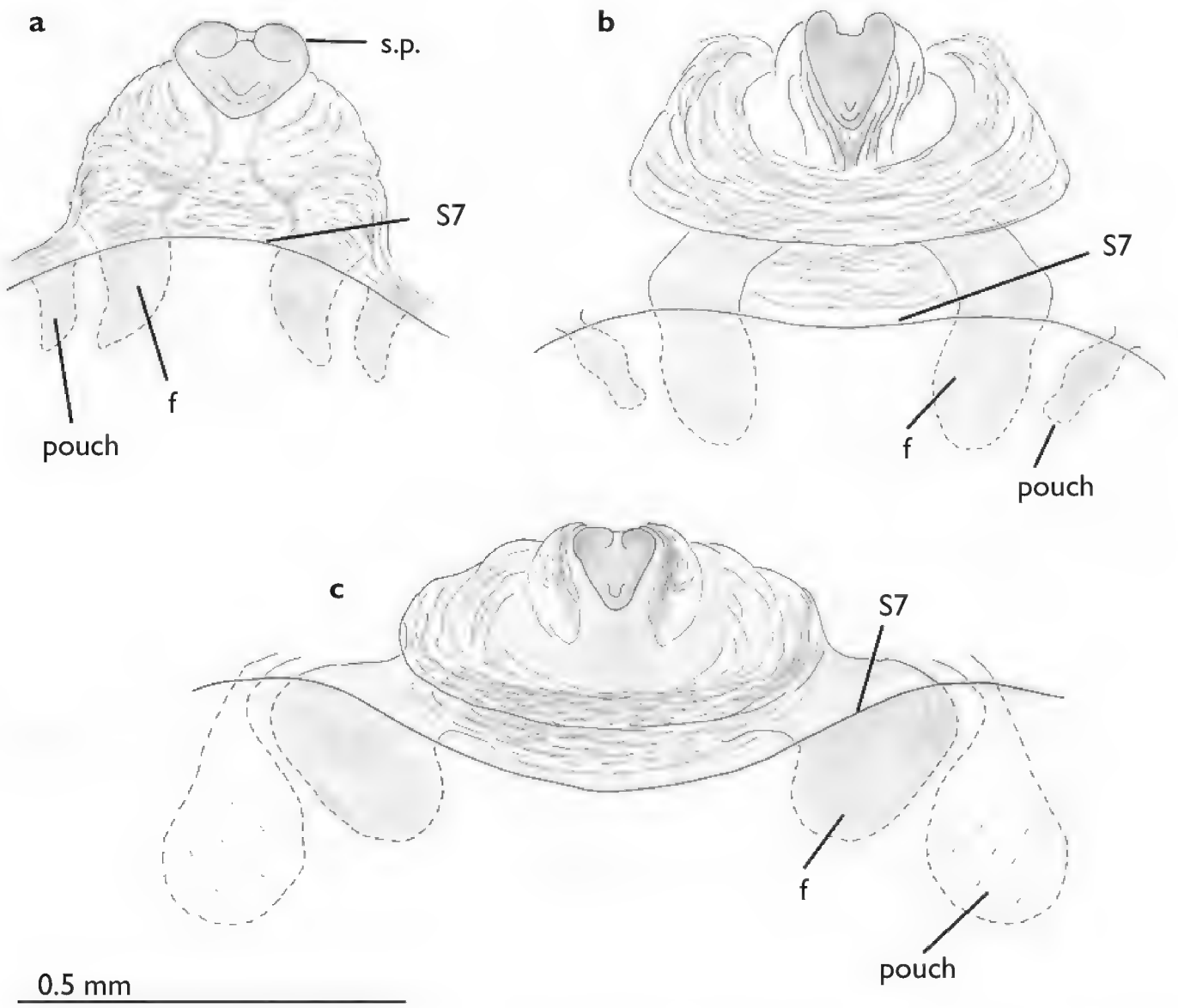

Figure 15. Subgenitale, ventral view. **a** *Chrysopodes* (*Neosuarius*) *nigripilosus* **b** *C.* (*N.*) *nigricubitus* **c** *C.* (*N.*) *pecki*. **f** membranous fold; **pouch** invaginated pouch **s.p.** sclerotized process at terminal end of subgenitale **S7** terminal margin of seventh sternite. The scale applies to all three images.

Scapes tan, unmarked; pedicel tan to light brown; flagellum tan. Venter: basilateral margins of submentum dark brown.

Thorax (Table 2; Fig. 3b). Pronotum (females) wider than long; large basal section without setae; cream-colored, with sublateral, mesal, mottled light brown markings. Meso-, metanota cream to light tan, without spots; setae on mesonotum, amber. Pleural areas cream-colored, without markings. Legs: setae amber.

Wings (Table 4; Figs 4, 5). Forewing about three times longer than tall. Costal area: greatest height ~0.17 times height of wing; tallest at costal cell (#4–5). Subcosta: two crossveins below stigma. Ten radial crossveins (between R and Rs); two rows of gradates; inner row with four gradates, outer row with six, both rows in regular, parallel pattern. Cubitus: icux2 curved, thickened, with small, bubble-like expansion mesally.

Hindwing narrow, length approximately three times height. Ten radial crossveins; four inner gradates; six outer gradate veins; three b cells; t cell present.

Forewing hyaline, very slight suffusion of brown to dark brown coloration around Rs at intersection with rcx1, first outer gradate, Cu near icu2. Subcostal crossveins

within stigma brown, surrounded with dark brown suffusion. Costal veinlets, gradates dark brown to black; ma1 black; icux2, small bubble-like swelling dark brown to black; marginal cell below 3A partially dark brown. Hindwing: stigma slightly opaque, veinlets within stigma brown, with brown pigment in surrounding membrane; icux2 cream-colored to light brown.

Abdomen (male & female) (Table 5; Figs 6, 11). Cream-colored, dorsally with faint, broken, brown mesal stripe, mottled brown spotting sublaterally; pleural regions cream-colored, without marks; sternites cream-colored, except S5, 6 (male) dark brown, S5 (female) dark brown; setae (female) cream-colored basally, brown distally; setae (male) long, cream-colored throughout. Tergites 6, 7: length: 2.3–3.0 (T6), 1.8–2.1 (T7) times greater than height (lateral view). Sternite 6: length ~0.9–1.0 times height. Spiracles ~0.05–0.06 mm diameter; atria noticably larger than spiracular openings.

Male (Table 5, Fig. 11). Apodeme of T9+ectoproct thin (dorsal apodeme): dorsal branch very heavily sclerotized basally, becoming abuptly thinner, extending upward, around and below callus cerci, fused mesally at top of tergite; ventral branch extending anteroventrally well into membrane below tergite, narrow, well-sclerotized, curving inward and invaginating distally; caudal branch with acute, unforked tip; tip with dorsal flange of heavy membrane. Callus cerci taller than wide (0.22 mm tall, 0.16 mm wide), with 30 trichobothria. S8+9 length 1.8 times proximal height; shape in lateral view: gradually tapering to truncate apex. Gonarcus: span near arch 0.39 mm, span between gonarcal arms distally 0.57 mm. Gonarcal arms long, narrow, ~0.39 mm length. Mediuncus: sclerotized surface slightly textured, with sparse microsetae; membrane immediately below beak (base of gonosaccus) smooth, tight, bearing setose glands; base of glands with small protuberances; gonosaccus delicate.

Female [Table 5, Fig. 15c; see *C.* (*N.*) *nigripilosus*, Figs 12, 13, 14]. Tergite 8: height of sclerite (including less sclerotized ventral extension) ~1.8 times length of sclerite. Ninth tergite + ectoproct (lateral view): distal margin with dorsal and ventral bulges. Callus cerci taller than broad (0.19 mm tall, 0.17 mm wide), with 35 trichobothria. Gonapophyses laterales ~0.5 times height of T9+ectoproct; 3.3 times taller than wide; orientated posteroventrally (~40° angle from midline). Subgenitale: base consisting of transversely folded, uninvaginated membrane, attached to terminus of S7; lateral margins of base with pair of sparsely setose, bulbous pouches, near, but separate from base of bursal glands; pouches slightly shorter than spermatheca. Bursal glands: with broad, elongate accessory ducts distally. Spermatheca: 0.13 mm diameter at mouth (distal end), 0.19 mm diameter in midsection (widest area), 0.6 mm long; invagination extending ~0.3 times length of spermatheca (length 0.17 mm). Spermathecal duct ~0.7 mm long (not including pale, brushy tip), after leaving subgenitale, bending right, becoming pale; distal ~1/10 brushy.

Type material. The holotype (a male, pinned) is in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., (USNM). The type locality is Ecuador, Galápagos Archipelago, Isla Isabela, Volcán Wolf, 4 km NE Puerto Bravo. The labels on the holotype read: (1) ECU: Galap: Isabela / V. Wolf, 4 km NE. P. Bravo / humid for, 17.V.96 / uv light / S. Peck, 96–192; (2) HOLOTYPE / *Chrysopodes* (*Neo-*

suarius) *pecki* Tauber & Tauber, des. 2010 [red]. There are two paratypes (females, in alcohol) in the Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium (IRSNB). Their labels read: (1) Ecuador, Galápagos Arch., Isla Isabela, Volcán Alcedo, SE crater rim at "Geyser", 1000 m, 3/IV/1996, L. Baert, K. Desender & J.-P. Maelfait, B96/0074; (2) PARATYPE / *Chrysopodes* (*Neosuarius*) *pecki* Tauber & Tauber, des. 2010 [yellow].

Etymology. The species is named in honor of Stewart B. Peck, Carlton University (Canada), in recognition of his contributions and devotion to the study of Galápagos insects.

Specimens examined. Type material only.

Intraspecific variation. Sample size very small, but see Tables 2, 4, and 5.

Undetermined specimen

There is a single specimen from Floreana (a male) that we were unable to place within any of the three species. Externally, it is very similar to *C.* (*N.*) *nigripilosus*, but the genitalia, in part, resemble those of *C.* (*N.*) *nigricubitus* and in part, they are unique. Specifically, the head coloration and markings are very similar to those of *C.* (*N.*) *nigripilosus* from Baltra; the dorsum is largely light brown and the pleural and ventral regions appear to be cream-colored as in the Baltra and Isabela populations. The membrane of the forewing has no markings or suffusion of pigment; the size and pattern of venation and thickened veins do not differ from those of *C.* (*N.*) *nigripilosus*; there are three crossveins below the stigma.

The genitalia resemble those of *C. nigricubitus* in that the gonaracus is relatively flat; the gonarcal arms extend laterally from the gonarcal bridge; and only the tips of the gonarcal arms bend downward toward the mediuncus. However, unlike any other specimens we have examined, the eversible pouches at the tip of S8+9 are relatively short, tapered distally, juxtaposed and partially fused mesally, and the membrane between the pouches is loose and large. Further study, especially analysis of the reproductive pheromones, might demonstrate that this is yet another undescribed, cryptic species.

Specimen examined: Floreana (= Charles, Santa Maria)**.** Black Beach, II/17/1964, R. L. Usinger (1M, CAS).

Discussion

The Galápagos lacewings. The two new cryptic species previously nestled within *C.* (*N.*) *nigripilosus* indicate that the Galápagos lacewing fauna may not be impoverished to the degree originally estimated. The number of named, endemic Galápagos *Chrysopodes* lacewings has increased from one to three species, and the possibility of another exists. Although clearly distinct, the Galápagos lineage of *Chrysopodes* shows marked af-

finities with the *Chrysopodes* (*Neosuarius*) fauna of the western Andean region – particularly the *C.* (*N.*) *flavescens* group to which it has been assigned (C. A. Tauber, in press).

Overall, including *Chrysoperla* [*Chrysoperla galapagoensis* (Banks, 1924)], four endemic chrysopid species are now documented from the Galápagos Islands. In addition, an endemic brown lacewing (Hemerobiidae) has been reported (*Megalomus darwini* Banks 1924) (Peck 2001). It is noteworthy: like many endemic Galápagos species of insects, at least four of the five endemic lacewings occur on more than one island. Thus, the pattern of a relatively depauperate, endemic arthropod fauna with broad inter-island distributions, noted by Linsley and Usinger (1966), Parkin et al. (1972), and Peck (2001), remains true for the Galápagos lacewings, but the number of recognized species has increased.

Each of the lacewing families is also represented by non-endemic, broadly ranging species on the Galápagos archipelago – Chrysopidae: *Chrysoperla externa* (Hagen, 1861) and *Ceraeochrysa cincta* (Schneider, 1851) and Hemerobiidae: *Sympherobius barberi* (Banks, 1903). All three of these species occur throughout Central and South America; one is also wide-ranging in the Pacific region. All are found on many of the Galápagos islands. [Note: *C. cincta* was erroneously reported to be endemic to the Galápagos Islands (Baert et al. 1992, Peck 2001); however, its distribution extends throughout Central and South America (Adams and Penny 1985).]

Comparison with the endemic lineages of Hawaiian lacewings. Statements regarding the low diversity of the Galápagos biota are particularly intriguing when the lacewings of the Galápagos are compared with those of another isolated Volcánic archipelago in the Pacific – the Hawaiian Islands. Hawai'i's extant endemic green lacewing fauna (Chrysopidae) consists of a single radiation of approximately 20 species in the monophyletic genus, *Anomalochrysa*. Among the endemic *Anomalochrysa*, 14 species are found only on a single island and only four species occur on three or more islands (Zimmerman 1957).

Hawai'i's endemic brown lacewing fauna (Hemerobiidae) consists of a similarly sized group of *Micromus* species that is presumed to be a single, monophyletic lineage. Among these species, sixteen are restricted to a single island and eight occur on more than one island (Zimmerman 1957, Monserrat 1993).

Unlike the Galápagos endemics, the endemic Hawaiian chrysopid and hemerobiid species are well differentiated; they are generally distinguishable by large external differences in morphology, as well as distinct genital differences among males (there are no reports on the female genitalia). Also unlike the Galápagos endemics, the geographic origins and phylogenetic relationships of *Anomalochrysa* and the Hawaiian lineage of *Micromus* remain unknown.

In summary: On the Hawaiian Islands, each of the two families of lacewings is represented by a single, diverse endemic lineage of unknown origins; each of the lineages currently contains ~20 well differentiated species, the majority of which are confined to a single island. In comparison, the Galápagos has three endemic "lineages" of lacewings, each stemming from the separate introduction of a genus known to inhabit the South American mainland. Two of "lineages" currently consist of only one described

species. The *Chrysopodes* (*Neosuarius*) lineage, consisting of three (perhaps four) species, also is small. In all three lineages, the degree of morphological differentiation is slight; differences between species are subtle, quite unlike the large interspecific variation within the endemic Hawaiian lineages.

There are numerous possible causes for the marked contrasts in the extent of radiation and the degree of diversification between the Hawaiian and Galápagos endemic lacewing lineages. Differences in the age, size, isolation, and ecological diversity of the island archipelagos may be factors; differences in the amount of time since the initial introductions, the especially harsh Galápagos environment and the biological characteristics of the original immigrant species are others to be considered.

Species relationships. The pattern of intraspecific and interspecific variation among the Galápagos lacewing specimens that we had on hand is noteworthy. In most cases, the differences among the species were consistent, and specimens could be easily and confidently identified to species. However, in one case, e.g., a male specimen in the series of *C.* (*N.*) *nigripilosus* from Pinta has particularly weakly pigmented wings and genitalia that resemble those of *C.* (*N.*) *nigripilosus*. As in some species of Darwin's finches on the Galápagos (Grant and Grant 2008), there may be a low incidence of hybridization between the *Chrysopodes* species.

Given the above, it is important to point out that in examining our *C.* (*N.*) *nigripilosus* and *C.* (*N.*) *nigricubitus* specimens carefully, we did not find morphological differences that would warrant splitting the group further. Nevertheless, a pattern of diversification and speciation without significant morphological changes has been well documented within several chrysopid taxa – e.g., *Chrysoperla*, *Chrysopa* (Tauber and Tauber 1997, Tauber et al. 1995, Henry et al. 2001). Thus, it is possible that additional cryptic species remain within any of the nominal *Chrysopodes* species on the Galápagos. The unique morphological characteristics of the male abdomen and genitalia (i.e., the large eversible pouches at the terminus of the abdomen and the setose ducts within the gonarcus) are consistent with reproduction involving chemical signals – long-range or contact pheromones. It has been demonstrated that changes in the chemistry of such signals in insects can result in reproductive isolation, without noticeable changes in morphology (long-range pheromones, e.g., Roelofs and Rooney 2003; contact pheromones: e.g., Grula et al. 1980). We hope that future studies will examine the variation in pheromone chemistry and molecular characteristics among the Galápagos lacewings.

Conservation. During the bicentennial celebrations of Darwin's life and his contributions, many well-founded pleas have been made for the continued protection and study of the Galápagos Islands and their unique flora and fauna (e.g., J. E. McCosker & R. H. Rosenblatt, Darwin and the Galápagos Symposium, AAAS, Pacific Region, Aug. 14–15, 2009, California Academy of Sciences, San Francisco). Our findings here, and the questions that they raise, add an additional, small but significant reason for supporting these international and national conservation efforts.

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